

## Chapter 12

# Collembola

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## I. INTRODUCTION

The Collembola are usually given the status of an Order in the Sub-Class Apterygota (Insecta). Imms (1936) considers that they are best regarded as an offshoot from the base of the early Symphylan stock, but stresses the remoteness of the group from the main evolutionary line of the Insecta. Ewing (1942), Wygodzinsky (1943), Jeannel (1949), Paclt (1954) and Ross (1955) give more recent assessments of the taxonomic position of the group, but, for the most part, agree with the conclusions of Imms.

While it is generally considered that the group retains rather primitive features, Gisin (1943), Delamare-Deboutteville (1950) and Paclt (1956) have suggested that many of these are adaptations to life in the soil; Delamare-Deboutteville points out that the persistence of primitive characteristics is typical of soil-living groups, and attributes this to the stability of the soil as an environment. Gilyarov (1949) suggests that aerial habitats were first colonized by insects via the soil.

Numerically the Collembola usually take second place only to the Acari in the air-breathing fauna of the soil, and on occasions (Stockli, 1943, 1946), they have been found to be even more numerous than the mites. Collembola

actually living in the soil spaces seldom exceed 3 mm in length, but the surface and litter forms may reach a length of 6–7 mm.

## II. SYSTEMATICS

The classification of Collembola is essentially due to Börner (1906), although great advances have been made in the taxonomy at the specific level during the past two decades. Such are these advances that in some cases, e.g. the Onychiuridae (Gisin 1952), where species groups exist, present workers are unable to make comparisons with much of the published data. It is important that ecologists should adopt the narrow species concept of Gisin, as further study of the biology of the genus *Onychiurus* (Hale, 1965a, b, c) has provided additional justification for it. J. P. C. Rowland (personal communication) has obtained further evidence in the form of the chromatographic separation of ninhydrin-positive substances in the *O. armatus* species group, where clear differences occur in 5 species of the group.

The keys of Stach (1947–1960) and Gisin (1960) are the most widely used for purposes of identification, and the latter author supplements his key by monthly additions and corrections in the form of leaflets entitled “Summarische Nachträge zu ‘Collembolenfauna Europas’”.

Collections are normally preserved in 70% alcohol, to which a little glycerol is added to prevent accidental desiccation. For specialized taxonomic purposes the best results are obtained by fixing in Gisin’s fixative (Gisin, 1960) for two days before mounting. Temporary mounts can be made in lactophenol; permanent preparations are best made either in Goto’s modification of polyvinyl lactophenol or using the method recommended by Gisin (1960).

## III. GEOGRAPHICAL DISTRIBUTION

Some species of Collembola, e.g. *Isotomurus palustris* (Müller, 1776) have a world-wide distribution, and in general Collembola have a more extensive distribution than the species of any other insect group. Probably this is due to two factors: first, they are easily dispersed by air or water currents or on the feet of birds; and, second, they are of great antiquity. Arthropods closely related to Collembola have been found in lower Devonian deposits in Scotland, whereas the first pterygote insects are from the upper Carboniferous. Salmon (1941) suggests a north European origin for Collembola, followed by an extension of the range in three directions: into Africa, North America and Australasia; and while the present-day distribution supports this hypothesis, it should be remembered that transportation by man has now greatly complicated, if not entirely masked, the original picture.

## IV. LIFE CYCLES

At high altitudes and in arctic or sub-arctic climates, Collembola have only one or two generations a year. Agrell (1941) records two generations in

*Folsomia quadrioculata* (Tullberg, 1871) in arctic Sweden, and the present writer, working on an area which experiences a sub-arctic climate in the northern Pennines, has found that most species have only one, or at the most two, generations a year (Hale, 1965b). At lower altitudes, and in more temperate climates, some species have several generations a year. Folsom (1916) records 3–4 generations in *Hypogastrura armata* (Nicolet, 1841) and Britt (1951) records a maximum of 12 generations a year in the same species kept in the laboratory at 24°C. The latter author indicates that the life span is about 2 months in *H. armata*, but that overwintering individuals live for about a year. Ripper (1930) records a life span of 5–10 months for Collembola of the genus *Hypogastrura*.

Even at high temperatures some species are limited to a single generation a year; this has been shown by Agrell (1941) in *Tomocerus vulgaris* (Tullberg, 1871) and by Bellinger (1954) in *T. flavescens* (Tullberg, 1871). Members of the Sminthuridae, even under sub-arctic conditions, tend to have more than one generation a year; Davidson (1934) records 4 generations during one year in *Sminthurus viridis* (Linné, 1758) under field conditions.

Estimates of the numbers of eggs laid by Collembola vary greatly. South (1959) records that a single female *Entomobrya multifasciata* (Tullberg, 1871) can lay up to six batches during a single period of laying, and each of these batches may contain up to 50 eggs. Under sub-arctic conditions probably fewer than 100 eggs are laid by most species of Collembola during the lifetime of a single female (Hale, 1965b).

While sexual reproduction is the normal method in most Collembola (Mayer, 1957), parthenogenesis is important in some species. Handschin (1928) referred to the possibility of parthenogenesis in Collembola, and suggested that the periodic appearances of large numbers of a single species might be considered as circumstantial evidence for it. Isolation of adult females of various species by Strebel (1932, 1938), Falkenhan (1932), Schaller (1953) and Mayer (1957) resulted in no young individuals being produced. In only one case, recorded by Lindemann (1950), in *Orchesella villosa* (Geoffroy, 1764), did an isolated female produce eggs which subsequently developed, and Mayer (1957) explains this by suggesting that spermatophores were introduced to the culture with the food. Subsequent to this, good evidence for parthenogenesis has been provided: in *Onychiurus parthenogeneticus* (Choudhuri, 1958) parthenogenesis is the normal form of reproduction, and males apparently do not exist in this species (Choudhuri, 1958); a form of parthenogenesis has been recorded in other members of the Onychiuridae by Hale (1965a, 1965b). Goto (1960) and Marshall and Kevan (1962) have demonstrated facultative parthenogenesis in *Folsomia candida* (Willem, 1902).

The study of life histories of Collembola often involves laboratory culturing; the method described by Goto (1961) has proved most efficient for this.

## V. FOOD

Whilst the identification of the gut contents of Collembola presents many problems, attempts have been made to determine the natural foods of these

insects. Strebel (1928) records decaying plant material, fungal mycelia, spores, dipteran pupae, other Collembola, parts of decaying earthworms and their own cast cuticles from the intestine of individuals of *Hypogastrura purpureescens* (Lubbock, 1867). Poole (1959) concluded, from gut analyses, that the larger species of Collembola fed mainly on soil fungi, whereas the smaller forms appeared to feed directly on the humus. No evidence has been found which suggests that different species of Collembola have different food preferences, and, in fact, the contrary seems to be the case: Agrell (1940) found the gut contents of one species to consist entirely of fungal mycelia in one area, and of amorphous detritus in another area.

The laboratory experiments of Dunger (1956) have shown that while Collembola were able to feed on fresh leaves, and conditioning of the leaves by micro-organisms was not a necessary preliminary, leaves which had been attacked by micro-organisms were eaten more readily. Schaller (1950) also found a preference for decaying leaves in *Tomocerus flavescens* and *Orchesella flavescens* (Bourlet, 1839). The variety of food material taken into the gut, and the preference for leaves attacked by micro-organisms, suggests that particles may be ingested, and apparently taken as food, because of the fungal mycelia, or other micro-organisms, that they contain. This is supported by observations of the present writer: after putting Collembola in to culture jars, which contain a mixture of plaster of Paris and powdered charcoal, it can be seen that after only a few hours their intestines contain particles of charcoal, and examination of the faecal pellets also reveals the presence of plaster of Paris. Often, too, yeasts appear to be passed through the gut unchanged. When the eggs hatch, the first instar individuals begin to feed immediately and often their intestines appear as black lines, the lumen being filled with particles of charcoal. Clearly neither the charcoal nor the plaster of Paris is ingested because of its nutritive value, but more probably because of the fungal mycelia growing over the surface; thus, everything that is taken into the gut of Collembola must not be regarded as food.

I. Healey (personal communication) has found that food preference experiments done in laboratory cultures provide little useful information. Probably this is a result of the unnatural conditions in the laboratory and the poor sensory equipment of the Collembola involved (*Onychiurus procampatus* Gisin, 1956), for this type of experiment. However, it was found that very high growth rates occurred when *O. procampatus* was fed on *Mortierella isabellina*, *Trichoderma viride* and *Phoma* sp.

## VI. SAMPLING AND EXTRACTION TECHNIQUES

Numerous methods have been used to remove Collembola from soil samples, and to date the most efficient methods are the high gradient cylinder of Macfadyen (1961) and the flotation method of Raw (1955). The latter method has the disadvantage of being suitable only for mineral soils, but Hale (1964) devised a similar method for use with organic soils.

For quantitative work, the present writer has found a sample unit size of

$10^{-3} \text{ m}^2$  to be most convenient. In most soil types this gives between 20 and 200 Collembola per core, which is a convenient number for counting and identification in a single session. On grassland areas between 15 and 30 such units taken on each sampling occasion give a standard error of the mean of about 5% of the value of the mean.

## VII. HORIZONTAL DISTRIBUTION

Glasgow (1939), Macfadyen (1952, 1957), Raw (1956), Hughes (1962), Kaczmarek (1960), Haarlov (1960) and Poole (1961) have all found that microarthropods tend to be aggregated in the soil.

Glasgow (1939) took samples in pairs, so that the edge of one sample touched the edge of the other. Comparing the variance between pairs with the variance within pairs, the former was found to be much the greater, indicating an aggregated population; this was shown in 4 species: *Onychiurus armatus* (Tullberg, 1869), *not sensu* Gisin, 1952; *O. ambulans* (Linné, 1758); *Tullbergia quadrispina* (Borner, 1901); and *T. krausbaueri* (Borner, 1901). Macfadyen (1952) found indications of aggregations in *Folsomia quadrioculata* from comparison of paired samples, but concluded that there was a very uniform distribution of microarthropods within each plant type examined. Kaczmarek (1960) defined the degree of aggregation by the percentage of samples in which the number of individuals was less than the mean, whilst Haarlov (1960) and Poole (1961) detected aggregation by the use of the coefficient of dispersion (Salt and Hollick, 1946).

The sizes of aggregations of Collembola have been estimated by Glasgow (1939); *Onychiurus armatus* aggregations were found to be between 3 inches (7.6 cm) and 12 inches (30.5 cm) in diameter, while in *O. ambulans*, *Tullbergia quadrispina* and *T. krausbaueri* the diameter was greater than 12 inches (30.5 cm).

Poole (1961) has attempted to show that aggregations of Collembola are not related to egg clusters, by comparing the egg batch sizes of different species with their coefficients of dispersion; the coefficient varies inversely with the egg batch size in all three cases. Comparison with data obtained by the present writer (Hale, in press) shows no clear correlation, and apparently aggregations may arise from gregariousness, egg batches, or the coming together of individuals at a food source. Swarming of Collembola on snow and water surfaces, as described by Davies (1932) and Paclt (1956), is probably a result of active gregariousness. Haarlov (1960) contends that the better the locomotory organs are developed, the less aggregated is the distribution of the species of Collembola in question, but the present writer has found no evidence to support this.

## VIII. VERTICAL DISTRIBUTION

Macfadyen (1957) has commented upon the fact that life tends to be concentrated where two phases meet, because of the photosynthetic demands of

the plants which form the primary food source. From the point of view of the soil microarthropods this has been demonstrated by Glasgow (1939), Agrell (1941), Gisin (1943), Nielsen (1949), Schaller (1949), van der Drift (1951), Murphy (1953), Bellinger (1954), Kuhnelt (1955) and Poole (1961), who have all shown that the highest densities occur in the upper layers of the soil. Other authors have correlated the depth distribution and size of microarthropods with the structure of the soil in which they have been collected. Schimitschek (1938), Stockli (1946), Weis-Fogh (1948), Kuhnelt (1950), Macfadyen (1952), Elton and Miller (1954), Haarlov (1955, 1960), Murphy (1955) and Klima (1956) have considered microarthropods in relation to soil structure, and have shown that the highest densities occur where the pore spaces are largest. According to Haarlov (1955) the cavity size decreases with depth in mineral soils, and here again the results show high densities in the upper layers of soil.

It has been shown in both mites and Collembola that changes in vertical distribution of different species occur throughout the year (Volz, 1934; Agrell, 1934; Jacot, 1936, 1940; Glasgow, 1939; Baweja, 1939; Strickland, 1947; Belfield, 1956; Schweizer, 1956; Stockli, 1957). In most cases this is interpreted as a vertical migration during periods of adverse climatic conditions in the upper layers of the soil, although it could, of course, be due to differential mortality. Frenzel (1936) and Dhillon and Gibson (1962) found no evidence of seasonal changes in distribution, and Leuthold (1961) has suggested the possibility of a diurnal rhythm in vertical movement.

#### IX. SEASONAL VARIATIONS IN NUMBERS

Before the work of Glasgow (1939), population studies of Collembola had been directed mainly at describing the fluctuations in large groups of species. Glasgow showed that different species reached maximum and minimum numbers at different times of the year, and thus the discrepancies (Table I) resulting when the work of different authors was compared could be explained. Table I summarizes the knowledge of the times of occurrence of peak numbers of microarthropods, with particular reference to Collembola. Most workers found an autumn peak, with low numbers in summer, although under arctic conditions Agrell (1941) and Hammer (1944) obtained summer peaks, as did Stockli (1957) in Switzerland and Poole (1961) in Wales. Bellinger (1954) found maxima at different times of the year in different species, and in this way these results compare with those of Glasgow (1939).

Since all work on the seasonal fluctuations of Collembola has been limited to two years or less, it has been found difficult to demonstrate a regular annual cycle.

#### X. COLLEMBOLA AS INDICATORS OF SOIL CONDITIONS

Gisin (1943) has suggested that different species of Collembola occur in soils of different degrees of acidity and quotes *Odontella armata* (Axelson,

1903) as typically basophil and *O. lamellifera* (Axelson, 1903) as strictly acidophil. Although some species are restricted to acidic or basic soils, this is not generally so, and many species, e.g. *Friesia mirabilis* (Tullberg, 1871), are equally common on acidic peats and base-rich soils.

TABLE I  
Summary of data on the seasonal distribution of Collembola and other microarthropods

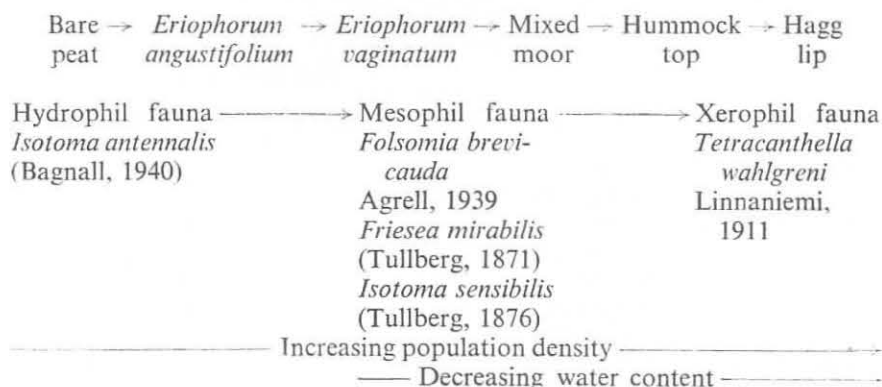
Author	Group	Peak populations			
		Spring	Summer	Autumn	Winter
Thompson (1924)	Total	—	—	—	×
	Arthropods				
Edwards (1929)	Total	—	—	Oct.	—
	Arthropods				
Ionescu (1932)	Protura	—	—	Oct.	Jan.
Frenzel (1936)	Mites and	×	—	Oct.	Jan.
	Collembola				
Ford (1937)	Collembola	—	—	—	Dec.-Feb.
Baweja (1939)	Collembola	—	—	Nov.	—
Glasgow (1939)	Collembola	April	—	Oct.	Dec.
Agrell (1941)	Collembola	—	× (Arctic)	—	—
Hammer (1944)	Mites and	—	× (Arctic)	—	—
	Collembola				
Weis-Fogh (1948)	Mites and	—	—	×	—
	Collembola				
Strenzke (1949)	Collembola	—	July	—	Dec.
Schaller (1949)	Collembola	—	—	Oct./Nov.	Jan.
Macfadyen (1952)	Mites and	—	—	—	Jan./Feb.
	Collembola				
Sheals (1957)	Collembola	—	—	Oct.	Dec.
Stockli (1957)	Mites and	—	×	—	—
	Collembola				
Poole (1961)	Collembola	—	Aug.	—	Feb.
Dhillon and Gibson (1962)	Mites and	May	—	Sept.	—
	Collembola				
Milne (1962)	Collembola	May/June	—	—	Dec.
Hale	Collembola	April/May (sub-arctic)	—	Nov./Dec. (sub-arctic)	—

× = Season but no month given; Spring=March to May; Summer=June to August; Autumn=September to November; Winter=December to February.

As Davies (1928) and Agrell (1941) have shown, probably the most important single factor governing the distribution of Collembola is humidity, and thus it is possible that Collembola may be used as indicators of the soil water conditions. Murphy (1955) and Hale (1963) have shown that changes in



populations of Collembola appear to be governed by physical factors which bring about changes in the water content of the habitat, and thus the species composition of a population can be related to the water content of the soil. In the case of eroding moor (Hale, 1963), this can be summarized in the following way, where soil types are indicated by their location and vegetation cover:



## XI. POPULATION DENSITIES

Published estimates of population densities vary greatly, and a summary of the available information is given in Table II. Glasgow (1939) has estimated that in some soils Collembola constitute up to 80% of the total numbers of animals, but, because of size differences, this is clearly no indication of their relative importance.

When the microdistribution of Collembola is considered, the specialized fauna associated with the hagg lip, on peat moorland, has afforded the highest densities yet recorded (Cragg, 1961; Hale, 1963). The maximum population density recorded by the present writer, from this area, was  $230,000 \pm 28,400/m^2$ , on 4 December, 1961; this figure was obtained from 15 sample units each  $10^{-3} m^2$  in surface area and 3 cm deep.

## XII. BIOMASS AND GENERAL METABOLISM

Although Collembola constitute a large numerical proportion of the fauna of most soil types, they constitute only a small percentage of the total biomass. From data obtained by the present writer, Cragg (1961) has compared the biomass and respiration of Collembola with other groups of the moorland soil fauna, and with two of the sites studied by Bornebusch (1930). These data are summarized in Table III. From this it can be seen that with regard to biomass and general metabolism the Collembola form a relatively unimportant part of the fauna of Limestone grassland and *Juncus squarrosus* grassland. However, on *Calluna* moor Collembola play a greater part



in the general metabolism. Biomass figures for mixed moor, obtained by the present writer, are little below those for Limestone grassland, i.e. about 0.4 g/m<sup>2</sup>, and Cragg (1961) has estimated that on this soil type Collembola account for 1.4% of the total biomass. Thus it appears to be on mixed moor that Collembola are of most importance on upland soils (from the point of

TABLE II  
Estimates of population densities from different soil types

Author	General habitat type	Vegetation and/or soil type	Density in thousands/m <sup>2</sup>
van der Drift (1951)	Forest soil	<i>Fagus mor</i>	0.7
Poole (1961)		<i>Pseudosuga</i> litter	40.0*
Forsslund (1945)	Heath	<i>Vaccinium</i>	15.0
Glasgow (1939)	Grasslands	<i>Dactylis</i>	27.0*
Salt <i>et al.</i> (1948)		Pasture soil	43.0
Weis-Fogh (1948)		Sandy soil	8.5
Schaller (1949)		Limestone grassland	15.9 and 25.0
Dhillon and Gibson (1962)		Loam on boulder clay	33.0*
Hale (1966)		Limestone grassland	53.0* (1960)
			42.0* (1961)
		Alluvial grassland <i>Juncus squarrosus</i>	44.0* (1960-61) 21.0*
Strenzke (1949)	Fen	<i>Phragmites</i>	20.0
Macfadyen (1952)		<i>Molinia</i>	25.0*
		<i>Deschampsia</i>	24.0*
		<i>Juncus subnodulosus</i>	7.2*
Hale	Moorland	<i>Calluna</i> litter	35.0*
Milne (1962)		Bracken	15.5* (1956)
			17.7* (1957)

\* Mean for 12 months (one year).

Note: only figures quoted in the literature after 1939 are given, as data collected before this date give very low estimates of population densities because of inefficiencies in the extraction methods used.

view of total metabolism). The figures quoted for Bornebusch (1930) seem much too high. Biomass figures of the order of ten times those recorded from the Moor House National Nature Reserve (W. G. Hale, unpublished) are claimed for populations fifty times smaller, when suitable corrections are made to convert the Bornebusch weighings of preserved material to live weights (see Nielsen, 1949).

Cragg (1961) points out that it is dangerous to make too detailed a comparison between the estimates of metabolic activity because the respiratory rates of animals under natural conditions are not known. Even so, it is clear that Collembola play a smaller part in the total soil metabolism than is suggested by the theoretical example for a meadow soil, constructed by Macfadyen (1957). In this example, Collembola account for 6.4% of the total biomass and 15.2% of the total metabolism in calories. Cragg (1961)

TABLE III  
A comparison of biomass (live weight) and respiration for two of the Bornebusch (1930) sites and two sites from Moor House, Westmorland (1840 ft O.D.). Modified from Cragg (1961)

Site and population density	Collembola		Total fauna	
	g/m <sup>2</sup>	Respiration (mg O <sub>2</sub> /m <sup>2</sup> /hr at 13°C)	g/m <sup>2</sup>	Respiration (mg O <sub>2</sub> /m <sup>2</sup> /hr at 13°C)
Limestone grassland 80,000/m <sup>2</sup>	0.6 (0.3%)	1.1 (2.0%)	189.7	54.9
<i>Juncus squarrosus</i> 12,000/m <sup>2</sup>	0.1 (0.1%)	0.3 (0.3%)	78.0	107.0
<i>Quercus</i> mull Bornebusch (1930). Site 10 493/m <sup>2</sup>	5.2 (5.8%) (0.10)	9.6 (25.5%) (0.19)	90.1 (76.8)	37.7 (17.7)
Spruce raw humus Bornebusch (1930). Site 8 2302/m <sup>2</sup>	6.8 (13.6%) (0.14)	20.0 (22.9%) (0.41)	50.0 (9.84)	87.4 (7.09)

Note: The data from Bornebusch (1930) have been corrected according to Nielsen (1949) and others; the original data appear below in brackets. While the corrections for "Total fauna" are probably more accurate than the original data, consideration of the population densities involved suggests that the original data are more nearly accurate for Collembola. The figures for respiration of Collembola are of the same order of magnitude as those obtained by I. Healey (personal communication) using the Cartesian diver.

has pointed out that this largely results from the relative absence of earthworms and enchytreids in Macfadyen's example. However, Macfadyen (1963) allows for earthworms and enchytreids in the analysis of the biomass and metabolism of a grassland habitat, and again quotes a high figure (13.4%) for the relative metabolic activity of Collembola. This figure is probably too high because of the method used for determining the weights of individual Collembola, and then calculating the total biomass by assuming a population of individuals all equivalent to adults in weight.

Calculations made by the present writer from weights of individuals of known instar, have shown that a population of 40,000 Collembola/m<sup>2</sup> is equivalent to a biomass of about 280 mg/m<sup>2</sup>, and I. Healey (personal communication) quotes a figure of 350 mg/m<sup>2</sup> for a population density of 40,000/m<sup>2</sup> on *Pteridium* moorland. These figures are appreciably less than those used

by Bornebusch (1930), Macfadyen (1957, 1963) and others in the estimation of metabolic activity in Collembola.

A further point is that because of the small percentage biomass of Collembola they can form only a relatively unimportant potential source of food for predators, and a relatively insignificant quantitative part of the total food web on most soils.

### XIII. THE EFFECT OF CLIMATE ON THE CONTRIBUTION TO THE SOIL TURNOVER

Apart from their metabolic activities during life, Collembola, like any other soil animals, contribute to the general soil turnover on dying, with the breakdown of the body by soil micro-organisms. Thus, where several generations occur each year, this type of contribution is greater than where few generations occur. In the sub-arctic climate of the northern Pennines only one, or at most two, generations occur each year, and metabolism is accelerated by higher temperatures and retarded by lower temperatures. Clearly, then, the annual contribution of Collembola at high altitudes is in this way smaller than in areas having a milder climate.

While many soil animals living under sub-arctic conditions are active at low temperatures, this is particularly noticeable in the Collembola, where there is apparently no diapause (at least in the Arthropleona), and most species are fully active just above freezing point (Kuhnelt, 1950). Choudhuri (1961) and South (1959) found threshold temperatures of about 4°C, below which no egg development occurred. The latter author also found that in the field, *Entomobrya multifasciata* laid only when the temperature exceeded 5°C, and laying ceased when temperatures fell below this level. The present writer (Hale, 1965b), working with Collembola collected from 2,000 ft o.d. in the northern Pennines, found that eggs would develop in a temperature as low as 2°C, and that some individuals laid eggs at temperatures not exceeding 3°C. While Choudhuri and South worked on Collembola from low-lying areas, the work of the present writer relates to Collembola living normally in a sub-arctic climate; it thus appears possible that there is a physiological mechanism allowing high-altitude forms to carry out biological processes at a temperature below those at which it is possible for the same processes to be carried out at lower altitudes, in a relatively warmer climate. It is thus possible that while contributing relatively little to the soil by way of decaying animal remains, Collembola contribute relatively more to the soil turnover at high altitudes than other groups, by remaining active at low temperatures.

### XIV. THE ROLE OF COLLEMBOLA IN SOIL FORMATION

In the living state, Collembola contribute to the soil in two different ways. First, they remove from it material which is ingested into the gut and, second, they produce faecal pellets which are added to the soil. Collembola have been recorded taking into their guts a variety of materials already described, and

their partial breakdown by Collembola may be an important factor in their being made more readily available to other decomposers. Stockli (1950), Dunger (1956, 1958) and Schuster (1956) have drawn attention to this aspect of soil formation by Collembola and mites and have considered their role in humus formation. Poole (1959) has suggested that Collembola play an important part in the dissemination of fungi, and in the breakdown of the faeces of larger arthropods. J. Doeksen (personal communication) and P. L. Hitchen (personal communication) have demonstrated the presence of a bacterium (*Bacillus* sp.) which breaks down chitin in the intestine of Collembola. Collembola eat their own cuticles, and it is possible that they ingest chitinous material in the form of remnants of other arthropods. In this way Collembola may play an important role in making chitinous material available again in the soil.

Zachariae (1963) has concluded that the contribution of Collembola to the mechanical and chemical breakdown of the soil is insignificant in forest soils. The weight of evidence suggests that this is, in fact, not so. In addition to what has already been said, there is the evidence of what has been termed by Muller (1879, 1884) "insect mull" soils. Probably the best known of these is the Alpine pitch rendzina of Kubiena (1953, 1955), where the  $A_1$  and  $A_2$  horizons are largely of coprogenous origin, with the presumed collembolan faeces forming a layer up to 30 cm deep. Schaller (1950) has calculated that populations of Collembola of the order of 100,000/m<sup>2</sup> produce 183 cc of faeces annually, which is equivalent to a layer 0.2 mm deep. However, this disregards breakdown by leaching and biological activity which, under the climatic conditions prevailing in the northern Pennines, would occur relatively quickly. G. Zachariae (personal communication) has expressed the opinion that the Alpine pitch rendzina has been produced not by Collembola but by Enchytraeidae. However, since no distinction can at present be made between the faecal pellets of the two groups, this cannot be regarded as established.

Kubiena (1955) has described how a coprogenous soil (Peat moder) can be derived from undecomposed peat, if the water table is lowered. While it is possible that Enchytraeidae may be responsible to a large extent for the formation of coprogenous soils, the density of mites and Collembola together exceeds that of Enchytraeidae in many areas, e.g. mixed moor (Cragg, 1961), so it seems reasonable to assume that they play at least an equal part in the accumulation of faecal material in such a situation.

On peat soils, the relative importance of Collembola is increased by the absence of earthworms and millipedes. According to van der Drift (1951), Kubiena (1955) and Blower (1956) millipedes are largely responsible for the formation of "mull-like moder" in some forest soils.

While on the face of it Collembola may not appear to be of great importance in the general soil turnover, it may be that in the comminution of plant residues and in their activity in raw humus they play an indispensable role; this aspect of the activity of Collembola in the soil should be carefully assessed in future work on the feeding activities of the group.

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